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INTEGRATING GENOME EDITING AND SPEED BREEDING FOR ACCELERATED SOYBEAN IMPROVEMENT IN INDIA: OPPORTUNITIES, CHALLENGES AND FUTURE PROSPECTS

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ABSTRACT

Soybean (*Glycine max* (L.) Merr.) accounts for about 69% of the global protein meal supply and approximately 30% of annual vegetable oil consumption, this signifies its indispensability to food systems worldwide. India's paradox is stark: approximately 12–13 million hectares under cultivation nearly 10% of global area, yet national average yields of barely 1.0–1.2 t/ha against a world mean of 2.8 t/ha and a documented attainable exceeding 4.0 t/ha. Conventional breeding has delivered real if incremental gains, but its pace is inadequate for a sector simultaneously contending with rapidly evolving pathogen populations, increasingly erratic monsoon patterns and heightened grain composition demands from processing industries. Genome editing (GE), particularly CRISPR-Cas systems and their derivatives, now offers the precision to modify specific loci in elite soybean cultivars without the lengthy introgression cycles that define conventional crossing. Speed breeding exploiting extended photoperiods, optimised temperature regimes and early seed harvest to achieve multiple crop generations per year provides an orthogonal strategy to compress the breeding timeline independently of genetic modification. This review critically examines India's soybean production constraints, evaluates the scientific progress underpinning GE and speed breeding as applied to soybean, and assesses key gene targets relevant to Indian conditions including Yellow Mosaic Disease (YMD) resistance, drought and heat tolerance, seed composition improvement and biological nitrogen fixation efficiency. The regulatory trajectory under India's emerging genome-edited plant guidelines is assessed, and research gaps, conflicting findings and unresolved technical challenges are discussed explicitly. Table 1 provides comparative soybean production statistics; Table 2 summarises GE events and gene targets relevant to Indian breeding objectives; Table 3 contrasts conventional and speed breeding parameters. Figures 1,2 and 3 depict the geographic distribution of soybean cultivation, the integrated GE–speed breeding pipeline, and the major genome editing targets relevant to Indian soybean improvement, respectively.

Keywords **:** soybean; CRISPR-Cas; speed breeding; genome editing; yield gap; India; biotic stress; abiotic stress; *Glycine max*

Introduction

Soybean (*Glycine max* (L.) Merr.), a short-day legume of East Asian origin, is now cultivated across more than 130 million hectares globally, with world production exceeding 370 million metric tonnes per annum (FAO, 2024). Its dual role as a protein meal source (approximately 44% crude protein in defatted meal) and an edible oil feedstock (approximately 18–20% oil content) makes it the economic fulcrum of global oilseed and feed markets (USDA-FAS, 2023). Roughly 85% of world soybean production enters animal feed channels; the remainder is divided among

food-grade processing, biofuel feedstock and industrial applications (Voora *et al*., 2020). India entered commercial soybean cultivation in earnest during the 1970s, driven by public breeding programmes, and by the mid-1980s the crop had become the dominant kharif cash crop across the central plateau states of Madhya Pradesh, Maharashtra and Rajasthan (Bhatia *et al*., 2008). Today India cultivates the crop across approximately 12–13 million hectares nearly a tenth of global area yet contributes only 3–4% of world production (SOPA, 2023). The arithmetic is unforgiving: India's yield of approximately 1.07 t/ha in 2022–23 was less than half the world average and barely a third of yields routinely achieved in Brazil and the United States (FAO, 2024).

This yield gap is not the product of any single limiting factor. It reflects an accumulation of biotic and abiotic constraints, agronomic deficiencies and the structural limitations of a breeding programme that has historically operated on timelines incompatible with rapid varietal turnover. Susceptibility to Yellow Mosaic Disease (YMD), caused by *Mungbean Yellow Mosaic India Virus* (MYMIV) and vectored by the whitefly *Bemisiatabaci*, can obliterate susceptible cultivars entirely in epidemic years. Intermittent and terminal drought during pod-filling, increasingly common under the erratic monsoon patterns that climate change is imposing on the central soybean belt, compounds the problem considerably (Deshmukh *et al*., 2014). The narrow genetic base of elite Indian soybean germplasm a legacy of domestication bottlenecks and decades of selection within a small pool of adapted lines limits the rate at which breeders can introgress beneficial alleles through conventional crossing (Varshney *et al*., 2021). Conventional variety development in India typically requires 10–15 years from the initial cross to commercial release, a timeline wholly inadequate given the speed at which pathogen biotypes are evolving and climatic conditions are shifting.

The past decade has seen GE technologies, above all the CRISPR-Cas9 system derived from the adaptive immune machinery of *Streptococcus pyogenes,* fundamentally expand what is achievable within a single breeding cycle (Doudna and Charpentier, 2014; Jinek *et al*., 2012). By directing a guide RNA to a complementary genomic sequence adjacent to a short protospacer-adjacent motif (PAM), the Cas9 nuclease introduces a site-specific double-strand break resolved by the cell's own repair machinery yielding targeted indel mutations through non-homologous end joining or precise substitutions through homology-directed repair (Cong *et al*., 2013). In parallel, speed breeding, formalized as a plant breeding platform by Watson *et al*. (2018), exploits 22-hour photoperiods, optimized temperature regimes and early seed harvest to achieve up to six generations per year in soybean under controlled conditions, compared with one or two under Indian field conditions. Used together, these two technologies allow precise genetic changes to be introduced and then fixed into homozygous elite backgrounds in a fraction of the time that conventional breeding demands (Hickey *et al*., 2019).

This review is not intended as a comprehensive catalogue of GE events in soybean several excellent reviews have already served that function (Freitas-Alves *et al*., 2025; Li *et al*., 2024; Xu *et al*., 2020). Rather, our aim is to assess, critically and with an explicit Indian perspective, which GE targets and speed breeding adaptations are most tractable for addressing the constraints that actually limit soybean productivity on Indian farms. We also examine the regulatory and institutional dimensions that will shape how quickly these technologies reach farmers, and we are explicit about the research gaps and unresolved questions that must be addressed before the potential described in laboratory publications can translate into field level impact.

Soybean Cultivation in India: Status and Significance

Historical development and current distribution

The transformation of soybean from an experimental curiosity to the dominant kharif cash crop of India's central plateau occurred within roughly two decades. Three early public-sector varieties JS 335, PK 472 and MACS 58 released between the late 1970s and mid-1980s, demonstrated that the crop could generate reliable returns under central Indian conditions, and their adoption spread rapidly across Madhya Pradesh, Maharashtra and Rajasthan (Bhatia *et al*., 2008). Madhya Pradesh has remained the leading producer ever since; together, the three central plateau states consistently contribute over 90% of national soybean production. This degree of geographic concentration, though reflective of genuine agro-climatic suitability, makes the entire sector vulnerable to correlated production shocks whenever regional monsoons fail or YMD pressure spikes a fragility that has not received adequate attention in national breeding and policy agendas. Smaller but growing areas exist in Karnataka, Telangana and parts of the northeastern states, where agro-climatic conditions are broadly suitable; yet adoption in these regions remains constrained by the absence of adapted early-maturing varieties and by thin processing value chains. Developing cultivars for these

emerging soybean areas should rank as a higher breeding priority than it currently does. The geographic distribution of soybean cultivation across Indian states is illustrated in Figure 1.

Production statistics and the yield gap

Table 1 summarises soybean production metrics for India alongside major producing nations. India's national average yield of approximately 1.07 t/ha compares unfavourably not only with Brazil (3.57 t/ha) and the United States (3.16 t/ha) but even with the global average of 2.86 t/ha (FAO, 2024). Under optimal research station management in India itself, yields of 3.5–4.0 t/ha have been documented (Bhatia *et al*., 2008), confirming that the gap is not attributable to any inherent genetic ceiling in Indian germplasm but to the cumulative effect of stress susceptibility, suboptimal agronomy and poor input use at the farm level. Bridging even half this gap would add approximately seven million metric tonnes to domestic production annually, enough to substantially reduce India's dependence on imported soybean oil and meal. What the national average also fails to capture is the severe inter-annual variability: in epidemic YMD years, state-level averages in Madhya Pradesh can drop below 0.8 t/ha, while in favourable seasons they approach 1.3–1.4 t/ha. It is this unpredictability, as much as the depressed mean, that erodes farm income and discourages investment in productivity-enhancing inputs.

Table 1 : Comparative soybean production statistics across major producing nations (2022–23)

Country	Area (M ha)	Production (M MT)	Yield (t/ha)	Global share (%)	Source
Brazil	43.3	154.6	3.57	41.2	FAO, 2024
United States	35.9	113.3	3.16	30.2	FAO, 2024
Argentina	16.2	49.5	3.06	13.2	FAO, 2024
China	9.7	20.3	2.09	5.4	FAO, 2024
India	12.6	13.5	1.07	3.6	SOPA, 2023
World Average	—	~374.0	2.86	100	FAO, 2024

M ha: million hectares; M MT: million metric tonnes. Data from FAO (2024) and SOPA (2023).

Economic importance

More than five million farming households in central India rely on soybean as their primary kharif cash crop (SOPA, 2023). India's soybean crushing industry comprises over 350 plants with an installed capacity exceeding 40 million MT per year yet the chronic gap between installed capacity and actual throughput reveals the inadequacy of domestic supply and the scale of the economic opportunity that improved productivity would unlock (SOPA, 2023). Soybean meal is the preferred protein supplement for India's expanding poultry and aquaculture sectors, while soybean oil competes with imported palm and sunflower oil in the household cooking oil market. The connection between farm-level yield improvement and national food security is therefore direct and substantial, a point that should inform investment priorities for public agricultural research.

Production Constraints in Indian Soybean

Biotic stresses

YMD is without question the most economically damaging biotic constraint on Indian soybean. The causal agent, MYMIV a bipartite begomovirus transmitted in a persistent circulative manner by *Bemisiatabaci* can inflict yield losses ranging from 40% in partially susceptible cultivars to complete crop failure in highly susceptible ones during epidemic seasons (Deshmukh *et al*., 2014). The disease is particularly severe in the warm, humid conditions of the central soybean belt during kharif, and whitefly populations in these regions are further amplified by dense, continuous planting of susceptible host crops. Despite this well-documented threat, most widely grown cultivars carry inadequate resistance, and breeding progress toward durable YMD resistance through conventional methods has been frustratingly slow largely because resistance sources in the primary gene pool are limited and recombination with adapted backgrounds has proved difficult.

Soybean Mosaic Virus (SMV), transmitted by aphids chiefly *Aphis glycines* causes foliar mottling, pod distortion and yield losses of 8–50% depending on cultivar and infection timing. Charcoal rot (*Macrophominaphaseolina*) and pod blight (*Colletotrichum truncatum*) cause additional losses, particularly under drought-stressed or late-season conditions. Among insect pests, the girdle beetle (*Obereopsis brevis*), stem fly (*Melanagromyzasojae*), pod borer (*Helicoverpa armigera*) and tobacco caterpillar (*Spodoptera litura*) collectively inflict significant economic losses across the soybean belt. Whitefly-mediated virus transmission makes vector management inseparable from disease management a

complexity that single-trait breeding approaches cannot fully address. Soybean rust caused by *Phakopsorapachyrhizi*, though historically of lesser concern in India than in sub-Saharan Africa or South America, has expanded its range under warming temperatures and represents an emerging threat that should not be dismissed (Deshmukh *et al*., 2014).

Abiotic stresses

Drought remains the dominant abiotic constraint. The rainfed character of virtually all Indian soybean production means that yield is tightly coupled to the distribution and reliability of monsoon rainfall; intermittent dry spells during August and September coinciding with pod initiation and seed filling are particularly damaging to harvest index (Deshmukh *et al*., 2014). Terminal heat stress during flowering, with maximum daily temperatures frequently exceeding 35°C in the central plateau during June–July, causes pollen sterility, flower abortion and reduced seed set. These effects are projected to intensify as mean growing-season temperatures rise under future climate scenarios (Varshney *et al*., 2021; IPCC, 2022). Paradoxically, waterlogging during early kharif - a consequence of intense, short-duration rainfall events whose frequency is increasing - generates hypoxic root conditions that impair nodulation and nitrogen fixation efficiency, sometimes in the same season and in adjacent fields that also experience mid-season drought.

Soil constraints compound the picture considerably. Vertisols dominant in the central soybean belt crack upon desiccation, narrowing the tillage window and impeding uniform seedbed preparation. Soil acidity in parts of Maharashtra and Telangana reduces phosphorus availability and suppresses rhizobium activity. Widespread micronutrient deficiencies particularly iron and zinc further constrain yield potential. Taken together, Indian soybean faces what is arguably the most complex multi-stress environment of any major soybean-producing region. This argues strongly for multi-target, multiplex GE approaches rather than the sequential single-trait introgression strategies that have historically dominated public breeding programmes.

Genetic and breeding constraints

Cultivated soybean's gene pool is substantially narrower than that of its wild progenitor *Glycine soja*, a consequence of domestication bottlenecks and subsequent intensive selection. In India, the problem is compounded: elite adapted germplasm has been selected primarily within the narrow range of maturity groups suited to the central plateau kharif season groups MG IV through MG VI leaving limited genetic variation for traits such as photoperiod insensitivity, cold germination tolerance or deep root architecture (Bhatia *et al*., 2008). Conventional marker-assisted selection has delivered incremental gains, but the estimated rate of genetic improvement in yield of 0.5–1.0% per annum falls well short of what India's production trajectory demands under a changing climate (Varshney *et al*., 2021). A generation time of approximately 100–120 days under central Indian field conditions adds a further structural limit to the pace of conventional breeding cycles. Against this backdrop, speed breeding and GE are not merely interesting technologies from an Indian breeding perspective, they represent a genuine operational necessity.

Genome Editing in Soybean: Tools and Applications

CRISPR-Cas systems in soybean: an established but still maturing toolbox

The technical landscape of CRISPR-Cas tools in soybean including challenges specific to its allotetraploid genome has been comprehensively reviewed (Freitas-Alves *et al*., 2025; Li *et al*., 2024; Xu *et al*., 2020) and requires only selective treatment here, focused on what matters most for Indian applications. The canonical SpCas9 system directs a single guide RNA (sgRNA) to a 20-nucleotide genomic target sequence flanked by a 5'-NGG-3' PAM, whereupon Cas9 introduces a double-strand break resolved primarily through non-homologous end joining to yield small indel mutations (Jinek *et al*., 2012; Cong *et al*., 2013). This basic mechanism is well established. The more pertinent question for India is how efficiently and in which elite backgrounds it can be reliably deployed and on this point, the published literature is largely silent.

Soybean's allotetraploid genome (2n = 40; approximately 978 Mb), shaped by ancient polyploidy, presents the specific challenge that many target genes exist as two or more homeologous copies capable of functionally compensating for each other, making multiplex editing of paralogs a common necessity (Jacobs *et al*., 2015). Editing efficiencies have improved substantially since the first CRISPR-Cas9 work in soybean by Jacobs *et al*. (2015), with reported frequencies now ranging from a few percent to over 50% depending on locus and transformation method (Sun *et al*., 2015). These figures come almost exclusively from model-adapted or North American cultivar backgrounds, however. Translation of these protocols to the specific elite Indian cultivars that underpin national soybean production remains an

underexplored and critical gap one that must be addressed experimentally, not assumed.

Beyond canonical SpCas9, Cas12a (Cpf1) recognises a 5'-TTTV-3' PAM and generates staggered cuts, broadening the range of targetable sequences and offering distinct advantages for promoter editing to achieve quantitative variation in gene expression (Zhou *et al*., 2023; Kim *et al*., 2017). Base editors cytosine base editors (CBEs) converting C to T and adenine base editors (ABEs) converting A to G have been successfully applied in soybean multiple times without introducing double-strand breaks, reducing the risk of unintended large-scale genomic rearrangements (Cai *et al*., 2020; Huang *et al*., 2023; Niu *et al*., 2022, 2024). Prime editing, which combines a Cas9 nickase with an engineered reverse transcriptase to write specified sequences into a target locus, has been demonstrated in soybean; efficiency currently lags behind base editors and optimisation is ongoing (Lin *et al*., 2020; Freitas-Alves *et al*., 2025). For Indian public-sector programmes operating under resource constraints, the practical hierarchy is likely: CRISPR-Cas9 knockouts first for well-validated targets, base editors for allele conversions where double-strand break-free editing is preferred, and prime editing reserved for cases where neither approach is sufficient.

Delivery of CRISPR components has been achieved through *Agrobacterium*-mediated transformation, particle bombardment and, increasingly, ribonucleoprotein (RNP) delivery approaches that circumvent stable transgene integration entirely (DBT, 2022). This last method is of direct regulatory relevance: India's proposed SDN-1 exemption framework would potentially allow RNP-edited plants without integrated foreign DNA to sidestep the full GM regulatory pathway. Making RNP delivery work efficiently in elite Indian cultivar backgrounds should therefore be treated as both a technical and regulatory priority.

Trait targets relevant to India

Resistance to Yellow Mosaic Disease and other viral pathogens

MYMIV-mediated YMD is arguably the most urgent GE target for Indian soybean, yet it is also the one where published evidence is least direct. Editing of eukaryotic translation initiation factor 4E genes (*eIF4E*), whose protein products are exploited by both potyviruses and begomoviruses as host factors for replication and cell-to-cell movement, has conferred broad-spectrum virus resistance in cucumber and other crops without detectable yield penalty (Chandrasekaran *et al*., 2016). The analogous resistance potential of *GmeIF4E*-null soybean lines against Indian MYMIV biotypes, however, has not been directly demonstrated under Indian field conditions. This gap is significant: MYMIV is phylogenetically distinct from the begomoviruses against which *eIF4E* editing strategies were originally designed, and genomic variability among Indian MYMIV isolates is documented. Whether *eIF4E* modifications validated against other begomoviruses will confer resistance to the specific MYMIV variants circulating in India's soybean belt is an empirical question that cannot be answered by analogy alone. Conducting this experiment sequencing *GmeIF4E* homologs in Indian elite backgrounds, identifying the most suitable target isoforms for editing, and then challenging edited lines with local MYMIV isolates in contained field conditions is arguably the single most impactful experiment that Indian agricultural genomics groups could currently undertake.

In parallel, CRISPR-Cas9 knockout of *GmTAP1* conferred enhanced resistance to *Phytophthora sojae* (Liu *et al*., 2023), and multiplex knockout of Mildew Locus O (MLO) genes improved powdery mildew resistance (Bui *et al*., 2023). Loss-of-function of *GmSNAP02* confers resistance to soybean cyst nematode (Usovsky *et al*., 2023) not yet a major constraint in India's central soybean belt but of growing concern as cultivation expands into eastern states where nematode pressure is higher. These diverse editing events collectively illustrate that CRISPR-based disease resistance is achievable in soybean; deploying it against the pathogens that actually matter in India requires the sequence and functional validation work described above.

Drought and heat stress tolerance

The GmLHYs genes Myb-domain transcription factors orthologous to CCA1/LHY in *Arabidopsis thaliana* and core components of the soybean circadian clock function as negative regulators of drought tolerance by repressing abscisic acid responses. Quadruple knockout of GmLHYs significantly improved drought stress tolerance; critically, further analysis showed that inactivation of LHY1a and LHY1b among the four GmLHYs genes is sufficient to achieve this improvement (Wang *et al*., 2021). This distinction matters practically. Multiplex editing of two targets is considerably more tractable than four, reducing the off-target burden and simplifying the regulatory characterisation required for each edited line. *GmDREB2A;2*, a functional ortholog of the *Arabidopsis* DREB2A transcription factor, is strongly induced under drought stress, and overexpression of full-length or partial DREB2A improves physiological

performance under water deficiency (Marinho *et al*., 2022). Whether targeted promoter editing replacing constitutive with stress-inducible cis-regulatory elements could achieve comparable benefit without the growth penalties sometimes associated with constitutive overexpression warrants investigation under Indian field conditions.

CRISPR-Cas9 editing of *GmFAD2-1A* and *GmFAD2-1B* altered membrane lipid composition in ways that conferred improved thermotolerance (Haun *et al*., 2014), a finding relevant to the central soybean belt where maximum daily temperatures during the June–July flowering window frequently exceed the threshold for pollen viability. Whether these lipid compositional changes are sufficient to translate into measurable yield protection under the temperature regimes experienced in Madhya Pradesh and Vidarbha has not been explicitly tested; this represents a gap that field evaluation under Indian agroclimatic conditions must eventually fill.

Seed composition and anti-nutritional factors

Simultaneous CRISPR-Cas9 knockout of *GmFAD2-1A* and *GmFAD2-1B* elevated oleic acid content from roughly 20% to over 80% of total fatty acids, generating high-oleic soybean oil with substantially improved oxidative stability and health profile (Haun *et al*., 2014; Du *et al*., 2016). For India's edible oil processing sector which has long struggled against the inferior oxidative stability of conventionally extracted soybean oil compared with imported palm oil this modification has direct commercial relevance and could influence consumer preference. Editing of *GmRAFS2* and related stachyose synthase genes reduced raffinose-family oligosaccharides (RFOs), improving meal digestibility for poultry and aquaculture feeds (Cai *et al*., 2018). Kunitz trypsin inhibitor (*KTI3*), which inhibits trypsin and reduces protein bioavailability in meal, is encoded by a single seed-expressed gene (Jofuku *et al*., 1989); a GE-mediated knockout strategy would achieve functionally equivalent results to classical *ti* mutants but without the linkage drag inherent in conventional backcross introgression from non-adapted germplasm.

Similarly, triple null mutants for the three lipoxygenase genes (*LOX1*, *LOX2*, *LOX3*) responsible for beany off-flavours that restrict soybean consumption in processed food products in India have been characterised through conventional mutagenesis (Hajika *et al*., 1991). CRISPR-mediated multiplex knockout would provide the same phenotype in elite Indian cultivar backgrounds without the lengthy backcross programmes required to eliminate undesirable flanking alleles a meaningful time saving given how slowly conventional programmes move. The stacking of multiple seed quality edits (high oleic, low RFO, low LOX, low KTI) in a single elite background through multiplex GE is a realistic near-term objective that would substantially enhance the value of Indian soybean meal for domestic food and feed markets.

Nitrogen fixation and nodulation

Enhancing the efficiency of biological nitrogen fixation (BNF) between soybean and *Bradyrhizobium* species is a high priority for Indian conditions, where erratic nodulation under high soil temperatures and low phosphate availability is common and fertiliser input costs are a significant constraint on farm profitability. GmSTF3/4 and GmFTs have been identified as indispensable components of the light-dependent mobile shoot-to-root signal that controls nodulation initiation; overexpressing lines show enhanced nodule formation (Wang *et al*., 2021). GmPT7, a phosphate transporter localised in nodules, when overexpressed significantly increased nodulation and improved soybean yield by up to 36% under low-phosphate conditions (Chen *et al*., 2019) findings of direct relevance to the phosphorus-deficient vertisols prevalent across much of India's soybean belt. Whether the same yield benefits are achievable through targeted promoter editing rather than constitutive overexpression, avoiding potential pleiotropic effects, is a worthwhile question.

A particularly significant recent finding comes from Zhong *et al*. (2024): *cle1a/2a* mutants displayed moderately increased nodulation with balanced carbon allocation, translating to improved yield and protein content in field trials without the yield penalty that has historically plagued supernodulating mutants. This distinction optimised rather than excessive nodulation is critical and often overlooked. Supernodulation mutants have long been theoretically attractive but practically disappointing because the carbon cost of sustaining excessive nodule numbers erodes the yield benefit of enhanced nitrogen fixation. The *cle1a/2a* result suggests a more nuanced genetic route that could deliver genuine fieldlevel improvements. Explicit validation of this approach under Indian soil conditions, particularly in the phosphate-limited vertisol environments of the central soybean belt, should be an identified research priority in national soybean improvement programmes.

Yield components and plant architecture

Yield itself is a highly complex and environmentally plastic trait, emerging from the

interaction of photosynthesis efficiency, carbon and nitrogen allocation, plant architecture and reproductive success. Pod shattering causes significant pre-harvest losses in mechanised soybean production, and its economic importance will grow as India's agricultural mechanization continues. CRISPR-Cas9 knockout of the *Pod Dehiscence 1* (*PDH1*) gene significantly improved pod shattering resistance without affecting other major agronomic traits (Zhang *et al*., 2022) a clean, functionally validated modification well suited to rapid deployment through the integrated pipeline proposed below. GmMYB14 overexpression through promoter editing reduced plant height, internode length and petiole angle while increasing pod and seed number per plant, with field yield improvements and improved drought tolerance also reported (Chen *et al*., 2021). Whether these architectural benefits are robust across the diverse growing environments and soil types of India's soybean belt rather than under the near-controlled conditions in which most published experiments were conducted remains an open question. Multi-location field evaluation across diverse Indian environments is a non-negotiable step before any of these edited lines could be proposed for commercial deployment.Candidate gene targets for key Indian soybean improvement priorities are summarised in Table 2. The major candidate genes and their associated breeding objectives relevant to Indian soybean improvement are summarized in Figure 3.

Table 2 : Selected CRISPR-Cas genome editing events in soybean relevant to Indian production constraints

Target gene(s)	Trait / phenotype	Editing approach	Efficiency	Reference
GmFAD2-1A/1B	High oleic acid; thermotolerance	CRISPR-Cas9	5–20%	Haun *et al*., 2014; Du *et al*., 2016
GmeIF4E	Virus (SMV/begomovirus) resistance	CRISPR-Cas9	~12%	Chandrasekaran *et al*., 2016
GmFT2a/FT5a	Early flowering; regional adaptation	CRISPR-Cas9	4–57%	Cai *et al*., 2018, 2020
GmRAFS2	Reduced RFOs; improved digestibility	CRISPR-Cas9	~15%	Cai *et al*., 2018
E1/E1La/E1Lb	Photoperiod insensitivity; early maturity	CRISPR-Cas9	~30%	Gao *et al*., 2024; Tsubokura *et al*., 2014
GmLHYs (×4)	Drought tolerance; compact architecture	Multiplex Cas9	~18%	Wang *et al*., 2021
PDH1	Pod shattering resistance	CRISPR-Cas9	~8%	Zhang *et al*., 2022
GmTAP1	*Phytophthora* resistance	CRISPR-Cas9	~11%	Liu *et al*., 2023
MLO genes	Powdery mildew resistance	Multiplex Cas9	~14%	Bui *et al*., 2023
GmSNAP02	Soybean cyst nematode resistance	CRISPR-Cas9	~9%	Usovsky *et al*., 2023
KTI3	Reduced trypsin inhibitor; digestibility	Base editing (CBE)	~7%	Jofuku *et al*., 1989; Freitas-Alves *et al*., 2025
GmMYB14 (OE)	Improved architecture; yield; drought	Promoter editing	~10%	Chen *et al*., 2021

RFOs: raffinose-family oligosaccharides; SMV: soybean mosaic virus; CBE: cytosine base editor; OE: overexpression line via promoter modification. Efficiency values are approximate, from cited studies.

Speed Breeding for Soybean: Principles and Application in India

Concept and origins

Speed breeding exploits the plant's response to extended photoperiod and optimised temperature to collapse the interval between successive generations. In its formalised iteration developed by Watson *et al*. (2018) soybean grown under 22-hour photoperiod at approximately 28/22°C day/night temperatures with early seed harvest at physiological maturity completes its growth cycle in approximately 77 days, enabling up to five or six generations per year (Watson *et al*., 2018; Chiurugwi *et al*., 2019). The concept has roots in NASA-funded experiments from the 1980s that investigated continuous-light crop production for space life-support applications, and acceleration of generation cycling for wheat and barley had been explored in Australian and UK programmes before Watson *et al*. (2018) formalised it as a scalable breeding platform. What has changed is the availability of energy-efficient LED lighting technology that makes 22-hour photoperiods economically viable and reproducible at scale, and the integration of speed breeding with genomic selection and GE that multiplies its impact within the same programme cycle. Since 2018, speed breeding has been applied across wheat, barley, chickpea, canola and several orphan legumes, confirming that the approach is broadly adaptable beyond the temperate species in which it was first validated (Chiurugwi *et al*., 2019; Hickey *et al*., 2019).

The photoperiod challenge and its solution for Indian soybean

Soybean is a classically short-day plant: reproductive development requires nights exceeding a critical photoperiod threshold. This requirement, while essential for latitude adaptation in a crop grown across such a wide geographic range, is the central biological obstacle to speed breeding of Indian elite cultivars, which belong predominantly to maturity groups MG IV–VI and have relatively strict photoperiod responses (Xu *et al*., 2013). Two practical pathways exist, and their relative merits deserve explicit discussion rather than simple enumeration.

Using naturally day-neutral germplasm from high-latitude collections as parents suffers from the limitation that such material is poorly adapted to Indian growing conditions and likely carries unfavourable alleles for traits critical to Indian performance soil adaptation, biotic stress resistance, grain composition. Recovering agronomic performance through backcrossing after speed breeding cycles substantially erodes the time advantage that speed breeding was intended to provide. The more strategically sound approach for Indian programmes is CRISPR-mediated knockout of *E1* and its homologs *E1La/E1Lb*, which together account for 62–66% of flowering time variability in soybean (Tsubokura *et al*., 2014). Multiplex editing of *E1* and *E1Lb* using CRISPR-Cas resulted in accelerated flowering by more than 30 days under long-day conditions (Gao *et al*., 2024), providing a direct route to generating speed breeding-compatible versions of elite Indian cultivar backgrounds without sacrificing their agroclimatic adaptation. Ghosh *et al*. (2018) showed that soybean genotypes with reduced photoperiod sensitivity can complete their cycle within 77 days under 22-hour photoperiod, and identified LED spectral conditions optimal for consistent early flowering induction.

The implication for India is clear: generating photoperiod-insensitive derivatives of JS 335, NRC 37, MACS 450 and other elite Indian backgrounds through *E*-locus editing should be treated as foundational infrastructure work not an optional add-on for any institution planning a speed breeding programme. Development of dedicated speed breeding facilities at ICAR-IISR Indore and key State Agricultural Universities, while requiring capital investment in LED growth chambers and controlled-environment space, is achievable with resources and technology currently available in India. The absence of such facilities remains a more significant bottleneck than it is generally acknowledged to be in national soybean research planning documents.

Generation advancement and integration with genomic tools

The primary value of speed breeding lies in compressing the time required for generation advancement. For soybean improvement programmes at Indian institutions where a single field generation requires approximately five to six months, speed breeding offers the prospect of completing an equivalent number of generations in 12–14 months under controlled environments, cutting the time from cross to homozygous F6 line from approximately six years to around 18 months (Hickey *et al*., 2019). Table 3 contrasts key parameters of conventional and speed breeding for soybean.

Speed breeding's value is substantially amplified by integration with genomic selection (GS), a statistical approach that uses genome-wide marker information to predict breeding values for complex quantitative traits at the seedling stage enabling selection decisions within rapid generation cycles without waiting for phenotypic evaluation under field conditions (Juliana *et al*., 2019; Varshney *et al*., 2021). The combination is powerful precisely because it eliminates the phenotyping bottleneck that would otherwise constrain how aggressively breeders can select within compressed cycles. For complex traits like yield under drought stress which cannot be reliably assessed in a growth chamber GS predictions calibrated on field data from earlier programme cycles allow breeders to cull inferior lines at the seedling stage and retain only the most promising material for eventual field evaluation, achieving selection intensities and annual genetic gains substantially greater than those achievable under conventional field-based programmes (Juliana *et al*., 2019; Varshney *et al*., 2021).

Table 3 : Comparison of key breeding parameters: conventional versus speed breeding in soybean

Parameter	Conventional breeding	Speed breeding	Reference
Generations per year	1–2	4–6	Watson *et al*., 2018
Days to flowering	45–55 (field)	25–35 (LED chamber)	Ghosh *et al*., 2018
Days to harvest (per cycle)	110–120 (field)	60–80 (chamber)	Watson *et al*., 2018
Time to F6 line	~5–6 years	~12–18 months	Hickey *et al*., 2019
Variety development cycle	10–15 years	3–5 years	Varshney *et al*., 2021

Annual genetic gain potential	0.5–1.0%	2.0–3.5%	Juliana *et al*., 2019
Primary infrastructure requirement	Field / glasshouse	LED growth chambers	Chiurugwi *et al*., 2019

LED: light-emitting diode. Values are approximate and represent performance under well-optimized conditions. Actual outcomes vary by genotype and environment.

Integrating Genome Editing and Speed Breeding

A synergistic pipeline for Indian soybean improvement

The transformative potential of GE and speed breeding is not fully realised by either approach in isolation. Their combination into a single iterative pipeline is what makes them genuinely disruptive for Indian soybean improvement. The conceptual framework depicted in Figure 2 involves: identification of priority trait–gene associations through genomic and functional analysis of Indian soybean germplasm; design of CRISPR-Cas sgRNA constructs targeting those loci in elite Indian cultivar backgrounds; *Agrobacterium*- or biolistic-mediated transformation and regeneration to obtain T0 plants with confirmed on-target edits; advancement through T1 and T2 generations using speed breeding under controlled-environment facilities to obtain homozygous, transgene-free edited lines within 12–18 months; and multi-location field evaluation through the national coordinated variety trial system, followed by fast-track registration under India's Seeds Act.

The key advantage over purely conventional approaches is iterative multiplexing. Traits that would require sequential introgression cycles potentially spanning 20 or more years in a conventional programme can be introduced simultaneously through multiplex CRISPR editing and fixed to homozygosity in an elite Indian background within three to four years (Zhang *et al*., 2022). Stacking YMD resistance (*eIF4E* editing), drought tolerance (*GmLHY* editing) and seed quality improvements (*GmFAD2-1A/1B* editing and *LOX* knockouts) in a single crossing programme through conventional methods would require at minimum 15–20 years. The integrated GE–speed breeding pipeline makes the same objective achievable within five to six years, including regulatory evaluation. This is not an incremental improvement it is a categorical difference in the pace of varietal development. That potential is contingent, however, on resolving the transformation efficiency and photoperiod sensitivity bottlenecks discussed above. Without those solutions in place, the pipeline cannot function at the envisioned pace regardless of how sophisticated the upstream molecular biology becomes.

Lessons from parallel crop systems

Dedicated GE–speed breeding integration studies specifically in soybean remain limited, which itself represents a research gap that Indian and international groups should address. In wheat, CRISPR-Cas9 editing of yield-component genes combined with speed breeding allowed the development and pre-commercial evaluation of improved lines within approximately two years (Bhatta *et al*., 2021). In tomato, Kwon *et al*. (2020) combined CRISPR editing of domestication syndrome genes with rapid generation cycling to generate improved semi-wild lines within six months. These examples are not directly comparable to soybean wheat and tomato are considerably more amenable to transformation and regeneration but they establish that GE–speed breeding integration can genuinely compress breeding timelines to a fraction of what conventional approaches require. CRISPR-mediated editing of *E*-locus genes to generate speed breeding-compatible elite Indian lines is therefore not merely a means of improving photoperiod adaptation; it is an enabling step that unlocks the entire integrated pipeline and should be prioritised accordingly.

Regulatory Landscape in India

India's regulatory framework for genome-edited plants is in a state of active and consequential transition. The Genetic Engineering Appraisal Committee (GEAC) and the Review Committee on Genetic Manipulation (RCGM) under the Department of Biotechnology (DBT) issued draft guidelines in 2022 proposing a tiered regulatory approach: SDN-1 events producing only small indels with no exogenous DNA would be exempt from the full GM regulatory assessment, while SDN-2 events involving precise base changes or small insertions templated from the target organism's own genome would undergo simplified case-by-case review (DBT, 2022). This trajectory broadly aligns India's regulatory thinking with the product-based rather than process-based approaches adopted by Japan, Argentina (Whelan and Lema, 2015) and Australia. If enacted as proposed, a functional SDN-1 and SDN-2 exemption would substantially compress the pathway from edited line to farmer's field, reducing regulatory timelines from the 10–12 years associated with full GM regulation to perhaps five to seven years from project initiation (Varshney *et al*., 2021).

Several important caveats deserve acknowledgement. The draft guidelines had not been finalised as of the time of writing, and India's regulatory history with agricultural biotechnology includes extended periods of policy ambiguity that have deterred investment. The exemption is explicitly contingent on the absence of exogenous DNA in the final plant, making RNP delivery and subsequent segregation of the editing construct non-negotiable requirements for regulatory compliance under the SDN-1 pathway. Even under simplified regulation, multi-location field trials for biosafety and agronomic evaluation will likely require three to four years. The intellectual property landscape adds further complexity: foundational CRISPR patents are held primarily by US institutions, but humanitarian licensing provisions have generally allowed non-commercial public-sector breeding in developing countries to proceed without undue restriction (Huang *et al*., 2016). Proactive engagement between India's public breeding institutions and the Protection of Plant Varieties and Farmers' Rights Authority (PPV&FRA, 2001) to develop clear registration pathways for edited varieties would reduce uncertainty considerably for both developers and farmers.

Challenges and Research Gaps

Several technical bottlenecks currently limit the translation of GE and speed breeding to Indian field conditions, and candour about their severity is more productive than optimism about their tractability.

Transformation efficiency in soybean remains genotype-dependent and generally lower than in model species or North American commercial cultivars. Elite Indian cultivars adapted to central Indian conditions JS 335, MACS 450, NRC 37 and their derivatives often regenerate poorly under standard *Agrobacterium*-mediated transformation protocols, and published efficiency data for these specific backgrounds are almost entirely absent from the literature. Developing efficient, reproducible transformation protocols for key Indian elite cultivars is a clear priority that should attract dedicated institutional support at ICAR-IISR Indore and State Agricultural University laboratories (Homrich *et al*., 2012; Freitas-Alves *et al*., 2025). This is not a glamorous scientific problem, but it is a prerequisite for almost everything else discussed in this review.

Off-target editing, though substantially reduced by high-fidelity Cas9 variants and careful sgRNA design, requires verification by whole-genome re-sequencing of edited lines before regulatory submission. Building this analytical capacity within Indian agricultural research institutions is important infrastructure that does not currently exist at adequate scale (Chen *et al*., 2019). The functional validation of sgRNA targets against Indian biotypes of MYMIV which may differ at the sequence level from the begomoviruses against which published *eIF4E* editing strategies were designed is a critical prerequisite for YMD resistance through GE that has received insufficient attention. Systematic molecular epidemiological surveys of MYMIV sequence diversity across India's soybean belt should be conducted, and their results should directly inform sgRNA design. Adaptation of speed breeding protocols for photoperiod-sensitive elite Indian cultivars remains incomplete; systematic evaluation of photoperiod and temperature combinations that allow adequate flowering in key Indian maturity groups represents a gap addressable relatively quickly with existing controlled-environment capacity at institutions like ICAR-IISR Indore (Ghosh *et al*., 2018).

Beyond the technical, socio-economic constraints will shape the pace of uptake regardless of what the breeding pipeline delivers. Price competitiveness for domestic soybean against heavily subsidised palm oil imports, gaps in the processing value chain in emerging production areas, and limited familiarity among farmers and extension workers with improved variety characteristics can all slow adoption of superior material once it is registered and available. Farmer engagement, value chain development and clear public communication about the biological and regulatory differences between genome-edited and transgenic crops will be as important as the technical advances themselves a dimension that receives far less attention in scientific literature than it deserves.

Future Perspectives

Projecting the trajectory of soybean improvement in India over the next decade requires specificity about what is technically feasible, institutionally realistic and commercially viable rather than an exhaustive catalogue of emerging technologies.

Pangenome resources constructed from diverse Indian soybean accessions and wild *Glycine* relatives will expand the catalogue of natural alleles available as editing templates, providing novel targets relevant to Indian biotic and abiotic environments not present in the current reference genome derived from North American germplasm (Liu *et al*., 2020). The MYMIV resistance alleles, drought adaptation variants and soil acidity tolerance mechanisms accumulated in wild and primitive *Glycine* germplasm over millennia could serve as editing templates that would otherwise require years of conventional introgression. India's soybean

germplasm banks particularly those maintained at NBPGR and ICAR-IISR contain under-characterised material whose systematic functional genomic evaluation should rank as an explicit national research priority, not a background activity.

Synthetic promoter engineering modifying cis-regulatory elements by GE to achieve tissue-specific or stress-inducible expression of target genes offers a route to quantitative trait variation that avoids the pleiotropic penalties sometimes associated with constitutive overexpression (Xue *et al*., 2023; Zhou *et al*., 2023). For drought tolerance improvement in particular, where constitutive ABA pathway activation carries measurable growth and yield costs in non-stressed environments, converting constitutive into stress-inducible expression profiles through targeted promoter editing represents a conceptual advance over first-generation overexpression strategies. Nanoparticle-mediated RNP delivery and virus-induced gene editing approaches, which bypass stable transformation entirely, will be particularly valuable for editing directly in elite Indian cultivar backgrounds, circumventing tissue culture recalcitrance and enabling DNA-free editing fully consistent with SDN-1 regulatory requirements.

Integration of AI-assisted target discovery, automated speed breeding cycles and continuously updated genomic prediction models into a digitally connected breeding pipeline is technologically within reach on a ten-year horizon, given adequate institutional investment. India's ICAR Vision 2050 and the National Food Security Mission identify soybean yield improvement as a strategic priority (ICAR, 2022), providing at least a stated policy foundation though the historical gap between stated priority and allocated resources in Indian agricultural research must be acknowledged. Partnerships with CGIAR centres, particularly ICRISAT, and with advanced soybean programmes in Brazil and the United States, would accelerate progress in both functional genomics and precision breeding. Open-source licensing for foundational CRISPR tools, combined with publicly developed transformation protocols for Indian elite cultivar backgrounds, could democratize access across State Agricultural Universities and allow multiple regional programmes to contribute to the national breeding effort in parallel rather than sequentially a model that has worked effectively in wheat genomics and could be adapted for soybean.

Conclusions

India cultivates approximately 10% of global soybean area but contributes only 3–4% of world production. Closing even half the roughly 60% gap between India's national average yield and the global mean would add approximately seven million metric tonnes to domestic supply annually, with substantial implications for farm incomes across the central soybean belt and for India's broader food and nutritional security. This review has argued, on what we consider solid scientific ground, that the combination of CRISPR-Cas genome editing and speed breeding offers a technically credible and practically achievable path toward that goal.

The argument rests on specificity, not generality. CRISPR-Cas knockout or modification of *eIF4E* genes could provide durable resistance to MYMIV but only if sgRNA designs are validated against the specific MYMIV biotypes circulating in India's soybean belt. *GmLHY* editing can improve drought tolerance but the sufficiency of two-target rather than four-target knockout needs confirmation in Indian elite backgrounds under central Indian field conditions. Speed breeding can compress the F1-to-F6 timeline from six years to 18 months but only after photoperiod barriers in Indian elite cultivars are resolved through *E*-locus editing. None of these bottlenecks is insurmountable; all require focused, adequately funded experimental work that is not yet underway at the scale the national soybean improvement challenge demands.

The regulatory trajectory under India's DBT 2022 draft guidelines is broadly encouraging. A functional SDN-1 and SDN-2 exemption framework, combined with fast-track registration procedures under the Seeds Act for varieties developed through non-transgenic GE, could reduce the time from initial editing event to farmer's field to five to seven years approaching international competitive benchmarks. With sustained investment in transformation capacity for Indian elite genotypes, established speed breeding infrastructure at ICAR-IISR and associated State Agricultural Universities, off-target analysis capability within national research institutions and proactive regulatory engagement, the integrated GE–speed breeding pipeline holds realistic promise of elevating India's national soybean yield toward 2.5 t/ha within a decade. Whether that potential is realised will depend less on the technology than on the institutional commitment to deploy it.

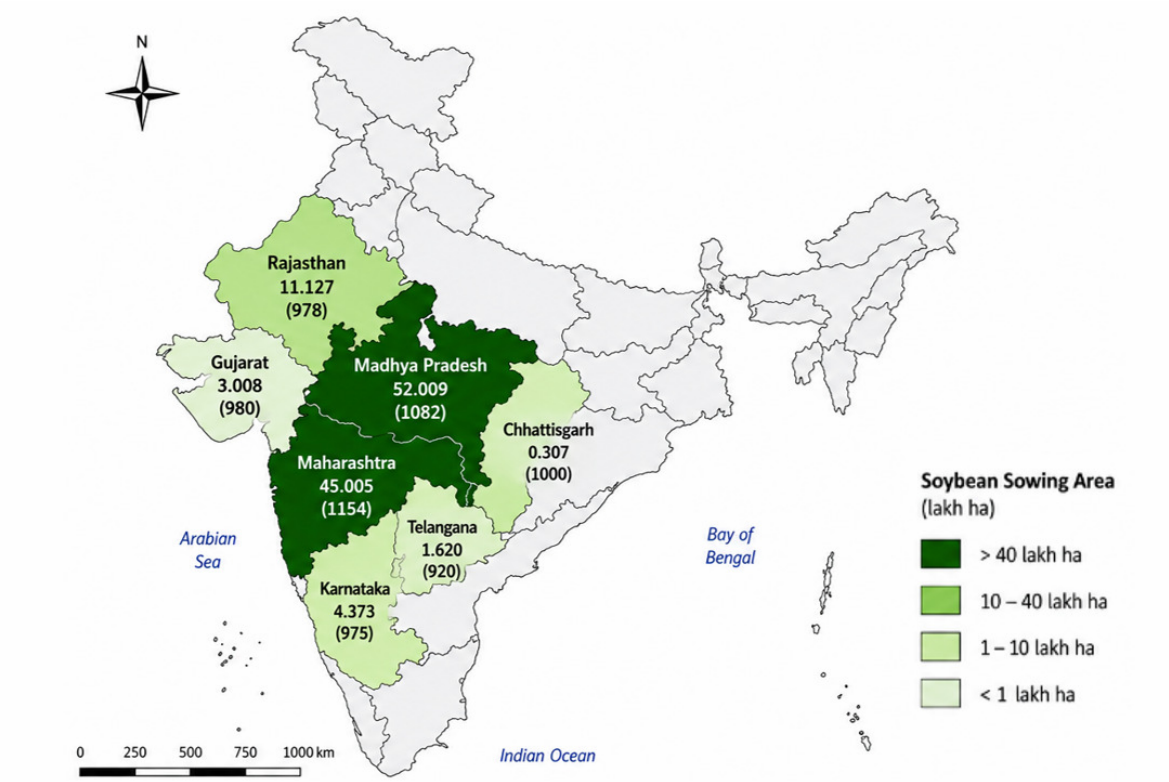

Fig. 1 : Geographic distribution of soybean cultivation in India based on state-wise sowing area and expected productivity during Kharif 2024. States are shaded according to soybean sowing area (lakh ha), while labels indicate expected productivity (kg ha^{-1}). Madhya Pradesh, Maharashtra and Rajasthan constitute the principal soybean-producing belt and together account for more than 90% of national soybean production. Data source: Soybean Processors Association of India (SOPA, 2024).

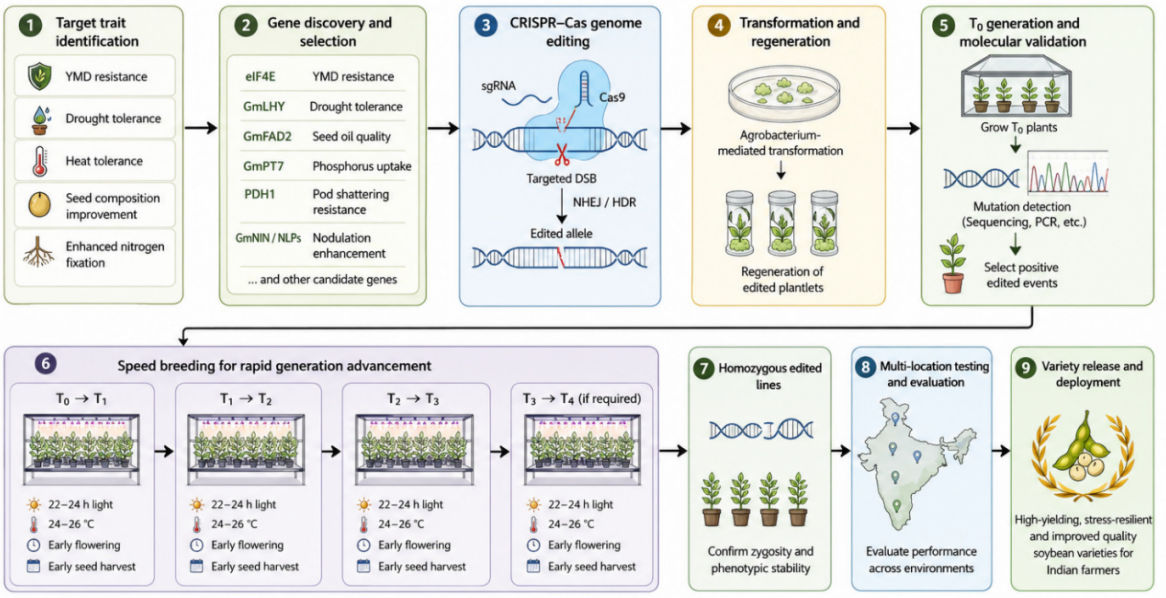

Fig. 2 : Genome editing and speed breeding pipeline for soybean improvement in India. The figure illustrates the workflow from genomic target identification through CRISPR editing, speed breeding-accelerated generation advancement, field-based multi-location evaluation and release of improved soybean cultivars.

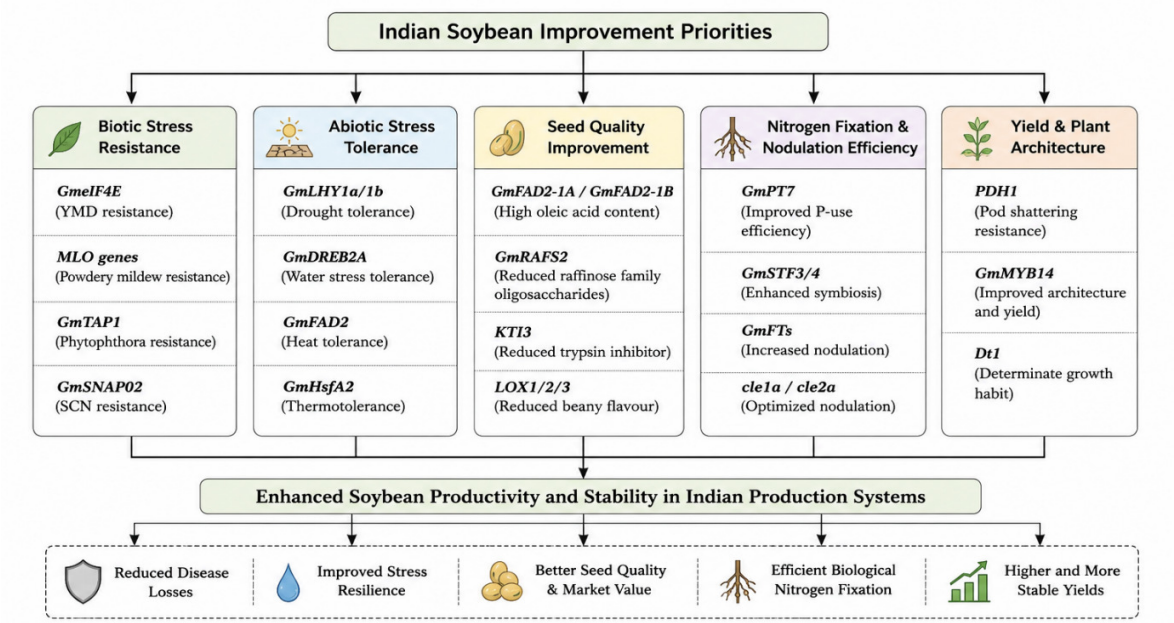

Fig. 3 : Major genome editing targets for soybean improvement under Indian production conditions. The figure summarizes key candidate genes associated with resistance to biotic stresses, tolerance to abiotic stresses, seed quality improvement, nitrogen fixation efficiency, and yield-related traits. Gene functions and associated breeding objectives are grouped according to their relevance to major production constraints in India's soybean-growing regions.

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